

Ultimately, how do these interactions affect the value of the metacommunity concept?

Our work in the pitcher-plant inquiline community has examined processes that occur at a variety of spatial scales: within an individual leaf, among leaves within an individual plant, among plants within a population, and among plant populations across the full geographic range of the species. This chapter presents an overview of such work by us and others, framed within the important components of metacommunity theory. After a description of the natural history of the community as a whole, we discuss spatial scales at which this community is appropriately studied, present natural patterns of variation and experiments conducted at each scale, and address the appropriateness of the metacommunity framework to each scale.

Natural History of Inquiline Communities

The purple pitcher plant, *Sarracenia purpurea*, is generally restricted to low-pH bogs from southern Canada to Florida (figure 5.1). The systematics of the species and, in fact, the entire genus are not well understood (Bayer et al. 1996). Two subspecies are recognized: *S. purpurea* ssp. *purpurea* is found north of Maryland and *S. purpurea* ssp. *venosa* from Maryland south at least through South Carolina (Schnell 1979; but see also Reveal 1993). Naczi et al. (1999) have recently proposed that the southernmost, somewhat disjunct, populations in northern Florida, southern Alabama, and southern Mississippi be considered a separate species, *Sarracenia rosea* (this group was sometimes formerly described as *S. purpurea* ssp. *venosa* var. *burkii*). As no differences in the inquiline communities associated with these subspecies are known (Buckley et al. 2003), we refer to the whole group as *S. purpurea* in the present chapter.

New leaves are produced by plants during much of the year, particularly just after flowering in the summer through the fall. The leaves are generally cup-shaped, with taller, narrower leaves produced in warmer climates (Ellison et al. 2004). Each leaf can contain from 0 to over 50 ml of rainwater and, in north Florida, survive for a year or longer. Leaves capture a large variety of invertebrate prey that may be attracted to nectar or by leaf coloration and drown in the water. The capture rate of insect visitors is apparently quite low (more than 99% of the visitors to each leaf escape; Newell and Nastase 1998); the successfully captured prey is composed primarily of ants (Heard 1998; Miller et al. 1994) but includes dipterans, collembolans (Cresswell 1991), and spiders (TEM, pers. observ.). The leaves of *S. purpurea* may produce digestive enzymes that aid in breaking down captured prey, especially in the first ten days after the leaf opens (Gallic and Chang 1997). Leaves vary in their ability to capture prey; larger pitchers may attract and consume more prey (Wolfe 1981; Cresswell 1993; but see Newell and Nastase 1998).

CHAPTER 5

Inquiline Communities in Pitcher Plants as a Prototypical Metacommunity

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Introduction

It has been argued that ecology is "awash in all manner of untested (and often untestable) models" with theory being developed too far ahead of its empirical support (Simberloff 1981). While this is an extreme view, it does appear that metacommunity theory has now matured sufficiently to require evaluation by means of experimental work, as Holyoak et al. and Law and Amarasekare argue in this volume. Experiments can test basic assumptions and predictions of metacommunity theory, while providing direction for future theory. For example, current metacommunity theory assumes that an understanding of some communities requires understanding the relative contributions of local and regional forces. However, if either force dominates to a large degree, simpler models are adequate to predict community dynamics and the metacommunity view is unnecessary. Such ties between theory and experimental work are critical to nurture the metacommunity concept as it develops.

The community found in water-filled leaves of the pitcher plant *Sarracenia purpurea* is an ideal system for testing assumptions and predictions associated with the metacommunity framework (see, e.g., Kneitel and Miller 2002, 2003). Local communities of invertebrates and bacteria in each leaf are discrete and easily manipulated. Species that inhabit pitcher-plant leaves have relatively short generation times (two hours to two weeks), allowing relatively short experiments to capture the dynamics of this system. The discrete nature of individual leaves, leaves on plants, and different plants in different bogs allows us to examine community variation across a variety of scales and the interactions of different processes at these scales.

We have used the inquiline system to begin to address a number of important questions about metacommunities. What constitutes a local community? What defines the boundaries of the larger metacommunity? What are the relative effects of species interactions and migration within and among communities? Are the rates of migration among discrete local communities appropriate for the metacommunity concept to be useful? Further, metacommunities are defined by the interaction between habitat and species, but different species, guilds, and trophic levels may interact with the environment at different spatial scales (Holt 1996).

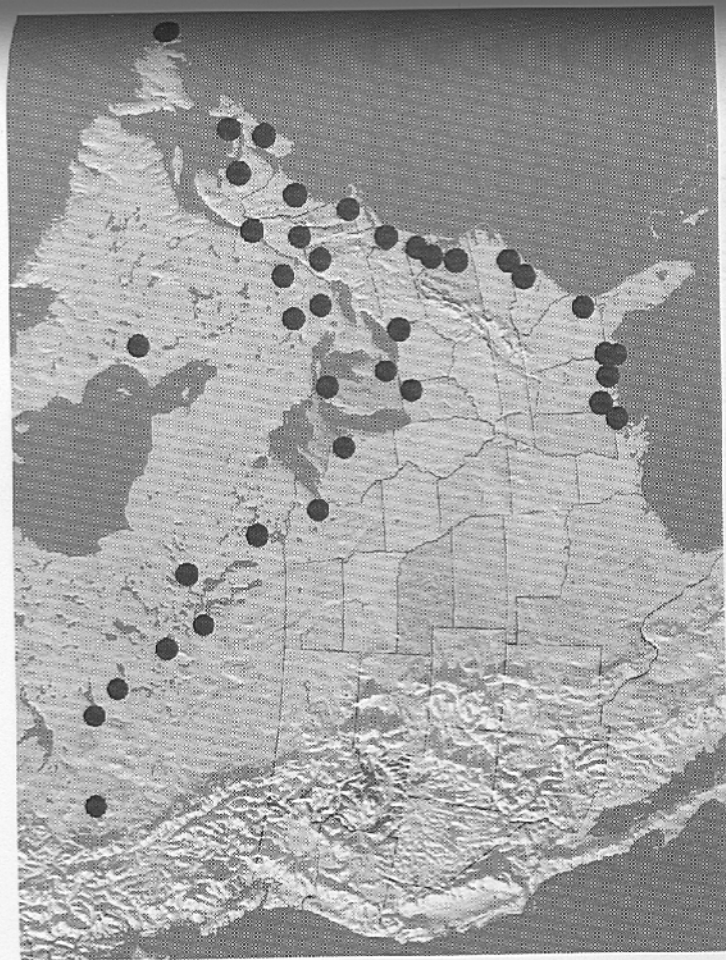


Figure 5.1 The distribution of *Sarracenia purpurea* across North America. Circles indicate populations that were sampled by Buckley et al. (2003), chosen to cover the range of the plant's distribution.

The individual leaves also act as hosts for an active community of nonprey invertebrates (inquilines), which are the subject of the present chapter (figure 5.2). Virtually all components of the community can appear within days after the leaf opens (TEM, pers. observ.; Judd 1959; but see Fish and Hall 1978). Inquiline species include several dipterans that occupy pitchers during their larval development: the pitcher-plant mosquito (*Wyeomyia smithii* [Coq.]), midge (*Metrionemus knabi* [Coq.]), and sarcophagid (*Fletcherimyia fletcheri* [Aldrich]). These species are univoltine in the northern distribution of *S. purpurea* but may go through several generations per year in the southeastern United States (Bradshaw and Lounibos 1972). The dipterans, along with the pitcher plant mite (*Sarracenia gibsoni* Nesbitt; Fashing and O'Connor 1984) and a bdelloid rotifer (*Habrotrachia rosa* Donner; Bateman 1987; Petersen et al. 1997; Bledzki and Ellison 1998), are found almost exclusively in *Sarracenia purpurea*. A number of other species are also commonly found in pitchers, including many species of protozoans (Addicott 1974; Cochran-Stafira and von Ende 1998), copepods, cladocerans (Miller et al. 1994; Hamilton et al. 2000), and bacteria (Addicott 1974; Prankevicus and Cameron 1989, 1991; Cochran-Stafira and von Ende 1998).

Each leaf must undergo succession after it is formed, so one might expect community (or leaf) age to explain much of the variation in community composition. In a greenhouse study, Fish and Hall (1978) found that individual leaves underwent a very regular progression of assembly of bacteria, protozoa, and dipterans. They suggested that, after 100 days, the community essentially dies when all available resources are consumed and the univoltine dipteran larvae pupate and leave the leaf. In habitats with short growing seasons, such patterns may occur (but see Judd 1959), but we have found little evidence of such strong successional patterns in pitchers from north Florida. Our preliminary data suggest that leaves attract large numbers of ants and mosquitoes in the first few weeks after opening but that they continue to attract some prey and mosquitoes until the leaf senesces or is so damaged that it cannot hold water (figure 5.3). Average leaf age is over 180 days, and many leaves survive more than a year. We suggest that, as pitchers get older, the effects of successional age on the inquiline community become relatively minimal compared to the effects of stochastic prey capture, mosquito deposition, and climate.

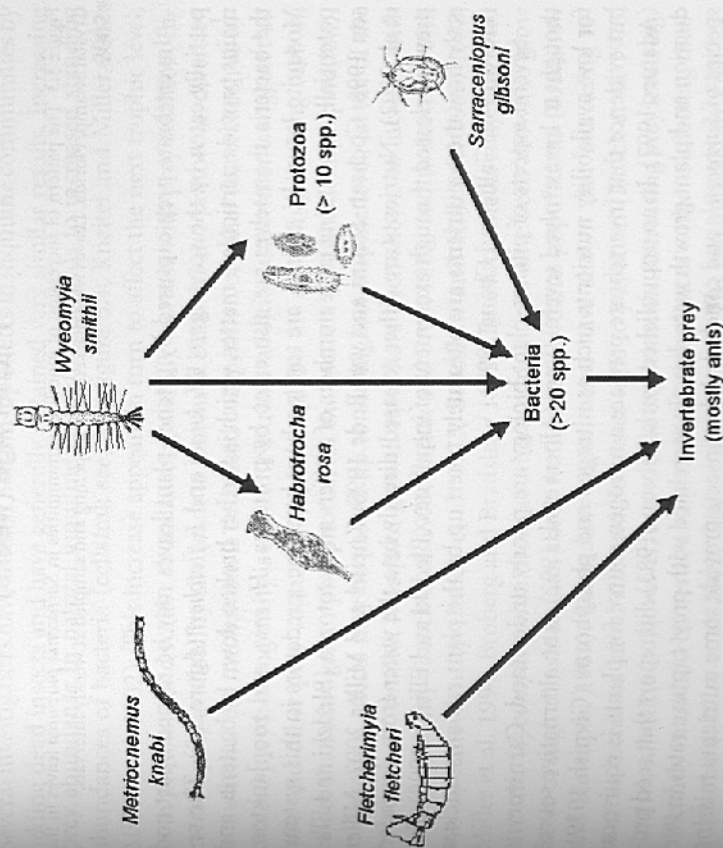


Figure 5.2 General food web of the inquilines found in *Sarracenia purpurea*. The species shown are numerically dominant both within and among leaves in populations of *S. purpurea*; other species, such as copepods, cladocerans, and nematodes, are generally rare. The plant's invertebrate prey (rather than primary productivity) serves as the base of the web, and mosquito larvae are at the top.

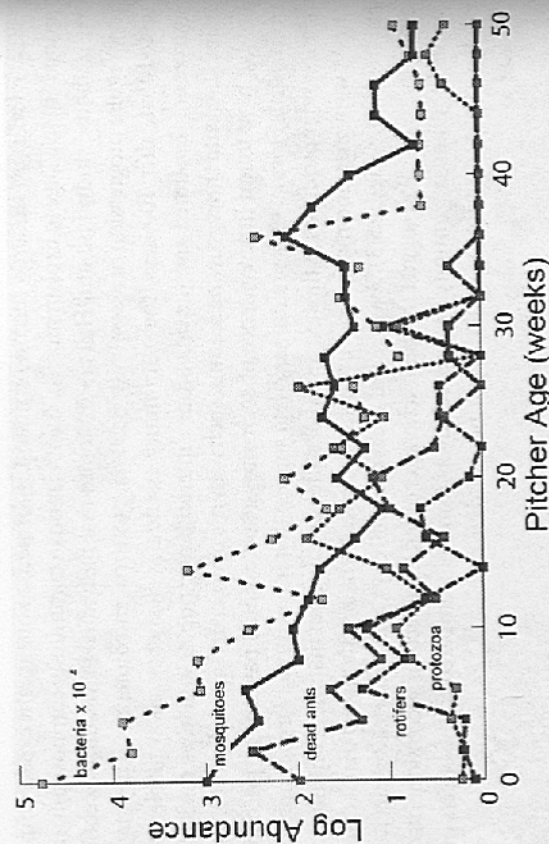


Figure 5.3 The pattern of succession of invertebrate communities in *Sarracenia purpurea* leaves in the Crystal Swamp, Florida. Leaves were marked before opening and sampled at weekly intervals.

Invertebrate prey captured by pitcher-plant leaves may be ripped apart and partially eaten by the scavengers, *M. knabi* and *F. fletcheri* (figure 5.2). The remains provide particulate matter, which is further broken down by bacteria, and the bacteria themselves are also eaten by protozoa, *H. rosa*, and zooplankton. Mosquito larva, *W. smithii*, are top, perhaps keystone, predators in this system, potentially consuming large numbers of rotifers and protozoa (Bledzki and Ellison 1998; Cochran-Stafira and von Ende 1998; Kneitel and Miller 2002; Miller et al. 2002). Nutrients are either released directly into the water from degraded prey or released through excrement of inquilines (Bledzki and Ellison 1998). Exactly how these nutrients are ultimately taken up by the plant remains unclear (Lloyd 1942; Gallie and Chang 1997).

Several aspects of pitcher-plant biology are poorly understood. Carnivory is thought to have evolved several times (Albert et al. 1992) as an alternative source for low-availability nutrients such as nitrogen and phosphorus (Givnish 1989), but evidence that invertebrate prey are a nitrogen source for plants is equivocal (Adamec 1997). In an unpublished work, Gibson (1983) did report that seed production and plant growth were directly correlated with prey-capture rates in two species of *Sarracenia* and concluded that insects provide some nutrients missing from bog soils. Chapin and Pastor (1995) measured the nitrogen obtained through prey capture in *S. purpurea* and found that it constituted as little as 10% of the total amount required. Similarly, both Eleuterius and Jones (1969) and

Christensen (1976) found that prey capture had little beneficial effect on plant growth. Although insects are generally thought to be the major carbon source for inquiline communities, at least two studies have mentioned the presence of minor amounts of filamentous green algae in some pitchers (Heard 1994b; Miller et al. 1994), and the bacterial assemblage may include a small number of photosynthetic species (Bradshaw and Creelman 1984; Cochran-Stafira and von Ende 1998) and nitrogen-fixing flavobacteria (Prankevicus and Cameron 1989; R. H. Reeves, pers. comm.). Clearly, the full relationship between the plant and the inquiline community found in its leaves has yet to be fully explored.

Within Pitcher: Local Dynamics

Ultimately, all community dynamics within an individual leaf are limited by productivity or the energy that comes into the system (Power 1992). Inquiline communities are distinctive in that they seldom include primary productivity; instead, they depend on detritus from the prey captured by the pitcher-plant leaf. Several investigators have studied bottom-up effects in inquiline communities by adding dead insects and have generally obtained very similar results. Increasing prey abundance in natural inquiline communities leads to increased standing abundances of bacteria (cells/ml; see, e.g., figure 5.4; Kneitel and Miller 2002; Miller et al. 2002). This increase appears in turn to affect the next trophic level; both protozoa and rotifer abundances generally increase with prey addition. Increased prey availability also leads to increased bacterial and protozoan diversity, but whether the mechanism is decreased competition or other factors such as increased prey heterogeneity is unclear. Nutrient-addition experiments suggest that ants and other prey captured by pitcher plants are providing limiting carbon, rather than nitrogen or phosphorus, for the bacteria (Gray et al. in preparation).

Resource effects may be passed up to the highest trophic level, larvae of the mosquito *W. smithii*. Mosquito growth rates have been shown to increase with food availability (Istock et al. 1975; Farkas and Brust 1985) and to decrease with intraspecific density (Istock et al. 1975; Bradshaw and Holzapfel 1986, 1992; Miller et al. 1994; Broberg and Bradshaw 1995). Resource effects may vary with latitude; *Wyeomyia smithii* from southern populations have been shown to grow faster at high densities than those from more northern populations (Bradshaw and Holzapfel 1989). Laboratory experiments have shown that increasing resources increases larval size and decreases time to pupation (Istock et al. 1975; Kneitel, submitted). However, in two field experiments, increasing prey levels significantly increased bacterial and protozoan abundances without affecting mosquito size (Miller et al. 2002; Gray et al. in prep.). The sarcophagid fly *Fletcherimyia fletcheri* may also be influenced by resource levels and intraspecific interactions (Forsyth and Robertson 1975), but the densities of their potentially cannibalistic larva are generally very low (less than one per leaf) unless supple-

mental food is provided (Rango 1999). Overall, the bottom-up control of dipterans by basal resources is generally indirect and diffuse and may often be relatively minor.

The relationship between the mosquito *W. smithii* and the midge *M. knabi* is complex. The presence of *M. knabi* has been shown to increase growth rates in *W. smithii*, apparently either directly by increasing the amount of particulate food in

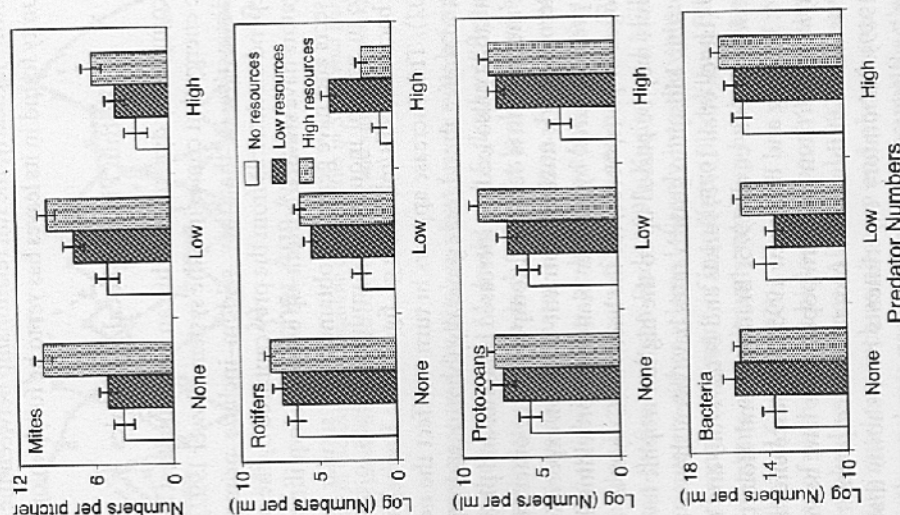


Figure 5.4 Effects of resources and predators on the abundances of several inquiline species in *Sarracenia purpurea* found in the Crystal Bog, Florida. We controlled resources by maintaining 0 (none), 5 (low), or 25 (high) ant carcasses per leaf; we controlled predator levels by maintaining 0 (none), 2 (low), or 10 (high) *Wyomyia smithii* larvae per leaf. Data shown are means and standard errors after twenty-three days (from Kneitel and Miller 2002). Mite and protozoan populations increased with increasing resource availability, but other groups were affected by complex combinations of indirect effects.

the water or indirectly by increasing bacterial numbers (Heard 1994a). *Metriocnemus knabi* may also feed selectively on larvae of other mosquito species, eliminating potential competitors of *W. smithii* (Petersen et al. 2000).

The composition of local communities is also affected by predation at several trophic levels. Experiments have demonstrated that a reduction in the abundance of the top predator, larvae of *W. smithii*, generally leads to increased abundances of their preferred prey, the rotifer *H. rosa*, as well as increased abundances of other prey, notably protozoa (figure 5.4; Addicott 1974; Cochran-Stafira and von Ende 1998; Kneitel and Miller 2002; Miller et al. 2002). Bledzki and Ellison (1998) documented that rotifer consumption by mosquitoes and sarcophagid flies was in direct proportion to rotifer density. In some cases, the effects of mosquitoes have been shown to cascade down trophic levels; increasing abundance of mosquito larvae has also been associated with increases in bacterial abundance (Miller et al. 2002) and richness (Kneitel and Miller 2002; Miller et al. 2002), apparently through decreases in the abundance of consumers in the middle trophic level.

Clearly, both bottom-up (resource-availability) and top-down (predation) forces are important in this community, as is probably true in many communities (Power 1992; Osenberg and Mittelbach 1996; Stiling and Rossi 1997). Resource availability and consumption by top predators could interact in a variety of ways through nonadditive effects on intermediate trophic levels. However, we have found that, in general, resources and predation have additive effects on abundances of bacteria, protozoa, and rotifers in inquiline communities (Kneitel and Miller 2002; Miller et al. 2002). An interaction between top-down and bottom-up forces was found only for protozoan species richness; predation decreased richness only at very low resource levels (Kneitel and Miller 2002).

Metacommunity Context: Our current view of metacommunities requires both local and regional processes and, in particular, that local forces such as competition and predation contribute to community patterns at local scales. Clearly, species interactions are important in inquiline communities; both predation and resource limitation operate to determine species abundances and richness. The question is therefore whether interactions at larger scales, such as migration and habitat destruction, are also important and require the integrative metacommunity perspective.

Among-Community Dynamics—Regional Forces

The communities found in different leaves in the same area vary widely in the presence and abundances of inquiline species (Harvey and Miller 1996). Some of this variation may be due to community age (figure 5.3), although age of the leaf is not always a good predictor of community composition (Miller et al. 1994; Buckley et al., 2004). More likely, variation among the communities found in leaves in the same area is due to aspects of the leaf that influence prey capture (e.g.,

leaf height; Cresswell 1991, 1993) or inquiline migration, especially of predators (Heard 1994a). Some of the variation may also arise from the inherently stochastic nature of prey capture and migration.

Migration can have several different effects on local communities in a metacommunity (Leibold and Miller 2004; Holyoak et al., chapter 1). First, low rates of migration can overcome migration limitation and allow species to disperse to new habitats. Second, migration among habitats with different conditions may allow species sorting, in which the conditions in each local community favor the growth and dominance of different species (Chesson 2000). Third, if rates are sufficiently high, migration may augment local population growth, allowing mass (Mouquet and Loreau 2002) or rescue (Brown and Kodric-Brown 1977) effects. Finally, relatively high rates of migration can have a homogenizing effect, allowing a smaller group of species to dominate regionally (Mouquet and Loreau 2002).

In pitcher plants, we think that at least the first two effects of migration, dispersal to open habitats and species sorting, are important. We know that initial colonists reach new leaves within days, if not hours, after they fill with water (figure 5.3; see also Judd 1959), but we know almost nothing about mechanisms of natural dispersal and the origins of dispersers. We can make several conjectures, however, based on the known natural history of these species. Some colonists, especially bacteria and protozoa, are probably generalists that may occur in soils or open waters in the area and disperse as propagules carried in the air. Others are obligate inquilines of *S. purpurea* (figure 5.2) that probably colonize from surrounding leaves. The dipterans (*W. smithii*, *M. knabi*, and *F. fletcheri*) can all disperse as adults. *Wyeomyia smithii* are apparently quite poor fliers but have been observed to lay single eggs in numerous leaves, preferring larger leaves with high numbers of either conspecific larvae or *M. knabi* (Heard 1994a). Further, *M. knabi* and *F. fletcheri* larvae have been observed crawling on wet surfaces on the outsides of leaves and may actively migrate from pitcher to pitcher. The component species in inquiline communities are therefore likely to have very different dispersal rates and distances.

Although migration limitation can be very important for metacommunity dynamics, very few experimental studies have demonstrated such limitation in any natural community (but see Shurin 2001). We used experimental introductions of several species of protozoa and the rotifer *H. rosa* into leaves to test for migration limitation in communities in which we manipulated resource and predator abundances (Miller et al. 2002). Three of the six protozoan species successfully became established after introduction; establishment rates were increased by high resource availability and the presence of predators (figure 5.5). The other three protozoan species and the rotifer failed to colonize any new communities; although all four are naturally found in these communities, some factor other than migration seems to limit their distribution. These results show that some

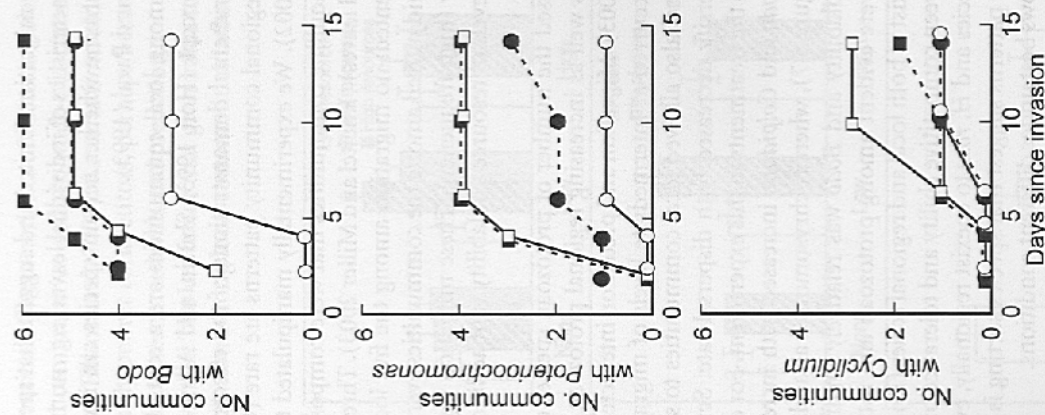


Figure 5.5 Numbers of communities successfully invaded over time by three protozoans (*Bodo* sp., *Poterionochromonas* [a chrysomonad], and *Cyclopidium* sp.) in manipulated pitcher-plant leaves in the Pleiophase Savanna near Sumatra, Florida. Solid squares denotes mosquito predators removed and prey added; solid circles denotes mosquito predators removed, no prey added; open squares denotes mosquitoes present, prey added; open circles denotes controls; mosquitoes present, no prey added (from Miller et al. 2002). Resource and predator levels affected invasion by different protozoans to different degrees.

inquire species are migration limited and suggest that species sorting may also occur, whereby characteristics of individual leaves (e.g., number of mosquitoes or prey captured) determine whether certain species can invade the community (Holt 1993; Tilman and Pacala 1993).

Dispersal rates among local communities are a central mechanism for the metacommunity concept (Holt 1993; Shurin and Allen 2001; Mouquet and Loreau 2002). Experimental demonstrations of the effects of varying dispersal rates on local and regional community patterns are rare (Gonzalez et al. 1998; Forbes and Chase 2002). We experimentally manipulated the rate of migration among regions of inquilin communities that were composed of five local communities (individual leaves) (Kneitel and Miller 2003). Three different migration levels were implemented: no migration among the five local communities and small amounts of fluid moved among the communities every two weeks (low frequency) and weekly (high frequency). These migration regimes were superimposed on different levels of resource availability (ant addition) and predator (*W. smithi*) abundance.

Migration increased the number of protozoan species co-occurring in each local community, as well as increasing regional protozoan diversity (figure 5.6; Kneitel and Miller 2003). Migration and predation interacted, such that the highest local diversity occurred at intermediate levels of migration when predators were absent. Dispersal also allowed local communities to share more species as the variance in diversity decreased with dispersal rate. Several species showed specific responses to the treatments in this experiment. For example, abundances of the protists *Colpoda* and *Colpidium* increased with increasing migration and food availability (figure 5.7), whereas chrysomonad abundances decreased with increasing food availability and *Rodo* was relatively unaffected by both treatments. Trade-offs were evident among protozoan and rotifer species and may allow species to coexist at both local and regional scales (Kneitel 2002). In particular, trade-offs between competitive ability and tolerance of predation appear to allow protozoan species and *H. rosa* to coexist regionally, even if few species can coexist locally. Such patterns suggest that species sorting is quite important and that each species grows best under different conditions.

Finally, community ecologists generally treat evolutionary change as something that happened a long time ago rather than as an active process. Although this static view may be a good assumption in some cases, many ecological processes occur over periods longer than a single generation of the component species, so understanding community patterns may require understanding evolutionary processes as well (McPeck and Miller 1996; Miller and Travis 1996). Particularly in a metacommunity context, migration provides gene flow among different communities, which can both provide genetic variation upon which selection can act and potentially swamp local adaptation. Preliminary work with bacteria in *S. purpurea* suggests that such local adaptation can occur and may

influence species interactions. Characteristics of bacteria isolated from one-week-old, early successional communities and six-week-old communities were compared in the laboratory (Ellison et al. 2003). Bacteria from older, established communities were frequently poorer competitors, perhaps because of a trade-off in the abilities to tolerate low resource levels and predation.

Metacommunity Context: The key factor that gives value to a metacommunity perspective is that migration among local communities influences local commu-

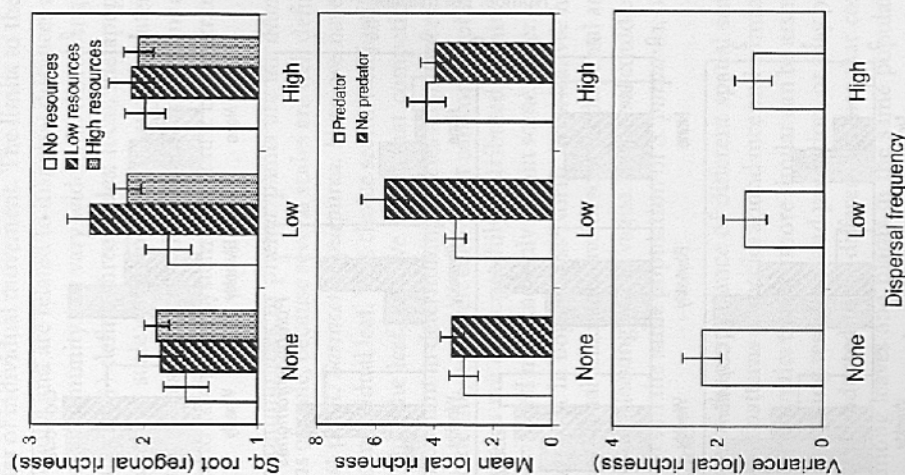


Figure 5.6 The effects of migration on within-leaf and among-leaf species richness and variance in species richness of protozoa in *Sarracenia purpurea* (from Kneitel and Miller 2003). Small amounts of fluid were moved among suites of five pitchers at either low (biweekly) or high (weekly) rates; the suites of pitchers were maintained either with or without mosquitoes present. Resource levels were as described in figure 5.4. The effect of migration on increasing local protozoan richness depends on the level of predation.

nity dynamics and patterns. In inquiline communities, some species have been shown to be migration limited, so even low rates of migration may allow the species to spread throughout a region. Further, migration has been shown to increase both local and regional species diversity and apparently interacts with local predation to determine the occurrence and abundance of species in the community. Understanding of the inquiline community thus requires a metacommunity perspective: local processes, regional migration, and regional heterogeneity all influence species distributions and abundances.

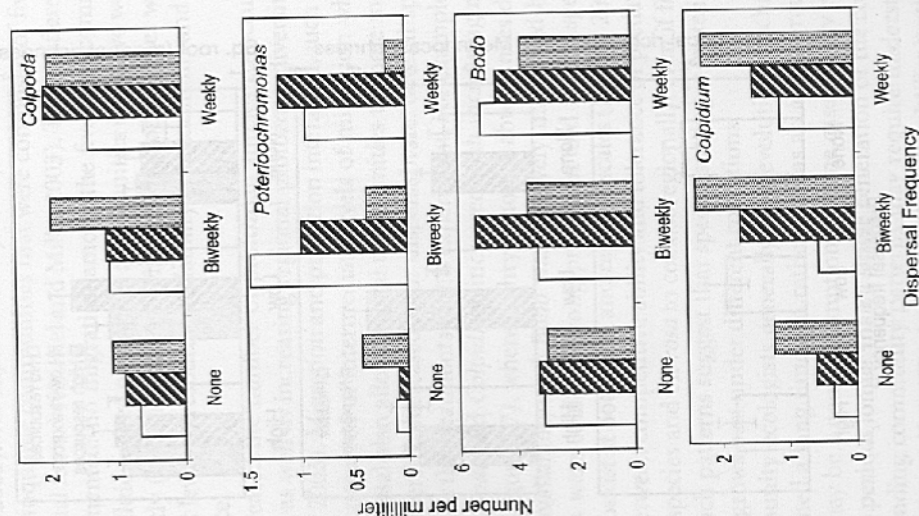


Figure 5.7 Effects of migration and resources on the abundances of several protozoan species in the inquiline communities of *Sarracenia purpurea* (from Kneitel and Miller 2003). Migration took place in small amounts of fluid moved among suites of five leaves at three levels: none, biweekly, and weekly. Resources were varied as described in figure 5.4. Abundances of *Colpoda* and *Colpidium* increased with increasing migration and food availability, whereas chrysomonad (*Pteriochironomias*) abundances decreased with increasing food availability, and *Bodo* was relatively unaffected by both treatments.

Larger-scale Dynamics

Although the metacommunity perspective adds a layer of complexity to our understanding of community dynamics, it still presents a gross oversimplification of the spatial structure of real communities. For most communities, the local and, especially, regional scales are vague constructs that probably represent points along a continuum rather than a true dichotomy. The local scale can be defined as where species interactions occur or in terms of some disjunction in the habitat that limits the rates of individual movement. The limits to the regional scale are more difficult to define and are related to dispersal distances and rates in which species in the same community can vary widely. In discussing metapopulations, Hanski and Gilpin (1991) define three scales: local, metapopulation, and geographic; the geographic scale encompasses distances greater than those over which an individual moves over its lifetime. Scale distinctions are therefore likely to be very specific to particular systems and must be arbitrarily defined by the researcher.

The inquiline communities in pitcher plants are an interesting system for studying questions of scale, because several scales are well defined by the natural history of the host plant, *Sarracenia purpurea*. Here, we have defined the local scale as that of the individual leaf. This choice seems well justified, as individuals can mix freely within the leaf, and we know that competition and predation within a leaf are important in determining species abundances. The regional scale is more difficult to define, however: each plant can consist of up to twelve water-filled leaves, the plants are often patchily distributed within populations, bogs themselves are distributed nonrandomly within some larger locality, and *S. purpurea* populations occur in bogs across North America. We have not been very specific about the regional scale but have described dispersal among leaves in the same area, intentionally leaving "area" vague. Dispersal could be among leaves on the same plant, leaves in the same population of *S. purpurea*, or even leaves from different populations.

Some indication of the importance of different spatial scales can be gained from a comparison of patterns of species abundance and community similarity at different scales. Communities that are more similar can be assumed to be affected by similar forces, including resources and predation, or may be linked by strong migration. We have conducted three different studies that compare patterns at different scales: among leaves and plants in the same population, among local populations, and among populations across North America.

We investigated spatial relationships among inquiline communities within a 10 m by 20 m area of the Crystal Bog in north Florida (Buckley et al. 2004). The locations of all 25 plants with a total of 141 water-filled leaves were mapped. For each leaf, we also determined length, aperture size, volume, and a rough estimate of relative age based on leaf position on the stem (Fish and Hall 1978). We partitioned the variance in species richness and abundance patterns into among-leaf

and among-plant components. Communities from leaves on the same plant were significantly more similar to one another, in terms of both diversity and species relative abundances, than leaves from different plants. The among-plant component explained 42% of the variance in invertebrate species richness and 34% of the variance in protozoan species richness, but the spatial positions of plants themselves had no significant effect on the community composition. In general, diversities within different functional groups were positively correlated; at both the among-leaf and among-plant scales, the species richness of bacteria and protozoa was significantly correlated with invertebrate richness, which was itself positively correlated with leaf length. Contrary to patterns of species richness, species abundances were not generally correlated with environmental variables such as leaf size, relative leaf age, number of leaves per plant, light availability, or soil moisture.

This study demonstrates that one important scale for inquiline communities is the plant itself but that, otherwise, the spatial position of leaves within the larger population was unimportant. Communities in leaves on the same plant may be influenced by similar habitat factors that we did not measure, migration among leaves on the same plant, or both.

Small distances can separate populations of *S. purpurea* within the same geographic area. Inquiline communities in these plant populations are likely to be subjected to similar environmental conditions and exchange migrants of at least some of their component species; both processes could result in greater community similarity between neighboring populations. Harvey and Miller (1996) quantified species patterns within leaves on the same plant and plants in the same area of the population in each of three different populations of *S. purpurea* in north Florida. Like Buckley et al. (2004), they found that leaves on the same plant were more similar than leaves on different plants, especially for bacterial communities, but different species demonstrated different spatial patterns, possibly as a result of different dispersal abilities. For example, neither plants in the same field nor populations of *S. purpurea* differed significantly in mosquito abundance, but populations differed in abundance of *M. knabi*, and areas within the same population of *S. purpurea* differed in cladoceran abundance.

At the largest scale, we can consider the distribution of the entire community type. The *S. purpurea* inquiline community is unusual in that the component species are thought to co-occur over the plant's entire range. This large range, up the eastern portion of North America from northern Florida to Labrador and across Canada to British Columbia and the Northwest Territories (figure 5.1), encompasses a wide range of climates, soil types, and hydrology. Further, because of glacial events, we can consider aspects of historical biogeography; *S. purpurea* is thought to have spread northward from its southern populations over the last 10,000 years, creating the habitat for the inquiline community as it spread (Ellison and Parker 2002).

The mosquito *W. smithii* has been especially well studied over the range of *S. purpurea* by Bradshaw, Holzapfel, and their colleagues (Bradshaw and Creelman 1984). They have demonstrated significant geographic variation in life-history traits of *W. smithii*, especially in developmental responses to day length (Bradshaw and Holzapfel 1989). *Wyeomyia smithii* also demonstrates significant changes in genetic structure; allozyme heterozygosity is greater in populations south of the maximum extent of the Laurentide ice sheet (Armbruster et al. 1998).

Less is known about how other inquiline species or whole community patterns vary over the range of the host plant. Buckley et al. (2003) visited thirty-nine sites across North America (figure 5.1), measuring both plant and inquiline community traits from twenty randomly chosen plants at each site. To minimize seasonal differences among the communities, they visited each site during the period of maximum leaf production, three to four weeks after the flowering of *S. purpurea*. Their study confirmed that, while leaves within a site may contain very different communities, among-site variation in the inquiline community is remarkably small across this large range; all the major species are found at virtually all sites, and only 4% of the total variation among 780 leaves investigated is explained by site (partial canonical correspondence analyses). Bacterial and protozoan species richness at among-leaf and among-site scales do increase with latitude (figure 5.8); numbers of species were significantly higher in the Canadian communities. Per-site invertebrate richness is not affected by latitude, and *W. smithii* abundances demonstrate a small but significant decline.

An interesting result is that this community is more variable in species composition at the within-site than at the among-site scale (Buckley et al. 2003). This pattern is unusual because at large scales we would expect to find that regional or biogeographic processes, such as dispersal, speciation, and landscape change over geological time, were more important than within-site variation in resource and predator abundances. Instead, the structure of this community at the among-site scale seems remarkably robust, despite a strong gradient in length of active season (eleven to twelve months in northern Florida to three months in the Northwest Territories), climate, soil conditions, and even life-history of dominant species (e.g., *W. smithii* and other dipterans are multivoltine in northern Florida but univoltine in northern populations). We do not know of any other community type that appears this stable or consistent over a range of this size or under growth conditions that vary to this degree, but few similar studies have been conducted.

Metacommunity Context: While the local scale appears to be well defined as that of an individual water-filled leaf, larger, regional scales are less discrete, and have different roles in a metacommunity framework. If we assume that dispersal rates decrease with distance between communities, then we can speculate that dispersal among leaves on the same plant or population of *S. purpurea* is relatively high and could be important for species sorting and mass effects (Leibold and Miller 2004). Migration among populations of *S. purpurea* in the same geo-

graphic area may be important for species sorting but is probably most important for overcoming dispersal limitation and allowing recolonization of some sites after disturbances such as drought or fire. Ultimately, however, this community type appears to have spread from the southeastern United States to Canada; migration among sites appears to have been sufficient to overcome migration limitation in entire populations of *S. purpurea*, leading to the remarkable uniformity of this community type across North America. We suggest that simple local versus regional partitioning of scale may be inappropriate for some, especially biogeographic, questions in community ecology.

Discussion: Are These Metacommunities? How Does One Deal with Scale Issues?

We began this chapter by suggesting that metacommunity theory has advanced sufficiently such that evaluations of its assumptions and predictions are needed from the field. We conclude that experiments have demonstrated that inquiline communities found in the water-filled leaves of the purple pitcher plant, *Sarracenia purpurea*, do indeed act as metacommunities with important interactions at different spatial scales.

At the local scale, competition for resources affects the abundances and richness of bacteria, protozoa (Cochran-Stafira and von Ende 1998; Kneitel and Miller 2002; Miller et al. 2002), and mosquitoes (Bradshaw and Holzapfel 1989; Miller et al. 1994). Further, predation by *W. smithii* affects the abundances and richness of its direct prey and may have cascading effects on bacterial abundance and richness (Addicott 1974; Cochran-Stafira and von Ende 1998; Kneitel and Miller 2002; Miller et al. 2002). Other, more complicated species interactions can occur at this local scale, such as the processing-chain mutualism (Heard 1994b). Interactions at the scale of the individual leaf habitat are clearly important in structuring these communities.

The structural habitat (individual leaves) itself provides a dynamic backdrop for this community. The birth-and-death dynamic of leaves creates a constant source of empty patches that drives one whole scale of interactions. Some inquiline species have now been shown to be migration limited (Miller et al. 2002). Migration has been shown to influence species richness and composition (Kneitel and Miller 2003). Further, the importance of migration can depend on the current occupants of the communities and their interactions with new migrants (Miller et al. 2002).

The metacommunity view of inquiline communities has not translated perfectly to the field and this may suggest areas for further theoretical work. Although the local community appears to be as well defined as that contained by an individual leaf, the regional scale is more difficult to determine and is almost certainly less discrete. We have not actually been able to follow migration from source to destination, so actual dispersal distances are still unknown. We do know that colonization can

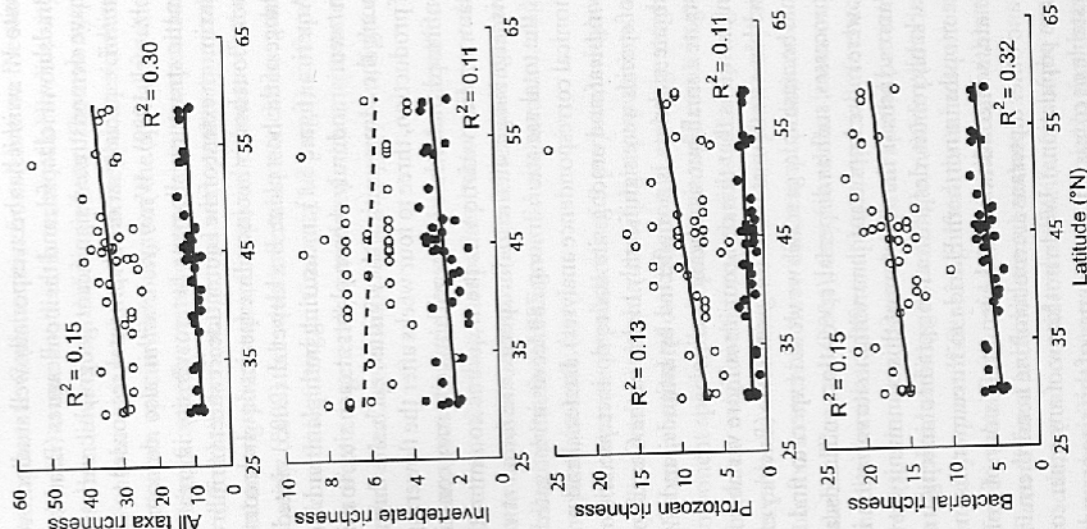


Figure 5.8 Relationships between latitude and species richness of inquiline species found in *Sarracenia purpurea* populations across North America for all species, invertebrates, protozoa, and bacteria at the among-site scale (open circles) and the pitcher scale (filled circles). Bacterial and protozoan species richness increase with latitude at both scales, but per-site invertebrate richness is not affected by latitude.

occur relatively quickly and bacteria seem not to be dispersal limited (Kneitel and Miller, unpublished data). Observational evidence suggests that, for some species, migration occurs primarily among leaves within a plant, but for other species, migration may span much longer distances (especially for the adult dipterans). The two alternative views of migration in this system are (1) that migration is simply a declining function of distance between leaves, and (2) that migration is best represented as a lottery in which species colonize pitchers from a large pool (air).

Even if we had a good knowledge of dispersal distances and rates in this community, it is likely that species have different migration functions, making a specific regional scale difficult to define. Species may fall into dispersal groups based on similarity in the mechanisms of dispersal or dispersal distance, but differences between groups must still be taken into account when the regional scale is defined. Further, the definition of any regional scale may depend on the questions of interest. For example, in a study of protozoan diversity, plants or local neighborhoods of plants may be the important regional scale, but entire populations of *S. purpurea* can be subject to occasional droughts and fires, so differences among populations may also be relevant. Local adaptation of inquilines in different populations may even occur and could affect invasion success in other populations. Large-scale or long-term questions may simply require larger, biogeographic, scales of study.

Are the communities associated with *Sarracenia purpurea* too unusual, even obscure, to yield results applicable to other community types? Very similar systems are found in other carnivorous plants. Naeem (1988), in a related system, found competitive interactions between midges (*M. edwardsi*) and mites (*Sarracenia darlingtoniae*) in the California pitcher plant, *Darlingtonia californica*. A variety of similar experiments have been conducted by Kitching (1987; Clarke and Kitching 1993) and others (Beaver 1985; Mogi and Yong 1992) in old-world pitcher plants (*Nepenthes* spp.) in Indonesia. The results from pitcher-plant experiments are also similar to studies in other phytotelmata, including tree holes (Srivastava and Lawton 1998) and the water-filled axils of bromeliads and other plants (review in Kitching 2000, 2001). Work to date on local interactions suggests that other container communities resemble our inquilin communities in harboring significant species interactions determined by both resources and predators; we know of no work on the regional processes in these systems. All the above studies are small aquatic communities whose energy input is allochthonous rather than arising through photosynthesis. The energy source may be less important than the discrete nature of the local community. The dynamics of other communities, both aquatic and terrestrial, with relatively discrete boundaries appear similar to those we find in pitcher-plant communities (e.g., Gonzalez, chapter 6; Cottenie and De Meester, chapter 8). Ultimately, we argue that the inquilin communities associated with *S. purpurea* are fairly typical, and represent a broad variety of natural communities.

Conclusions

In most communities, especially aquatic ones, processes such as competition and predation occur locally, driving the local abundances of most resident species (see, e.g., Forbes and Chase 2002). At some larger regional scale, however, most communities are subject to disturbance and habitat variation; colonization and migration may then be critical to persistence of some species in the region. An understanding of community composition and dynamics will require an understanding of processes important at both local and regional scales.

Work with the inquilin communities associated with *S. purpurea* demonstrates that species interact and patterns of species association occur at several spatial scales. Local scales may be the most easily defined and manipulated to demonstrate that habitat characteristics and species interactions affect local community composition. Larger, regional scales are also important but are more difficult to define because different trophic levels (and species within trophic levels) respond differently to processes on these scales.

Current metacommunity theory focuses on small-scale migration and ecological interactions as the important processes at the regional scale. We suggest that future theory should also consider two related lines of research: First, a variety of regional processes occurring at different scales must be recognized and investigated (Ricklefs 1987). These include migration among local communities, as well as very different factors such as species' historical spread and biogeography (Holt and Gomulkiewicz 1997). Researchers may have to abandon the simple local versus regional dichotomy in favor of something like multiple, nested, spatial scales (sensu Loreau and Mouquet 1999) and develop an understanding of the feedback dynamics between local community interactions and regional-scale movement patterns. Second, evolutionary processes should be integrated into our understanding of metacommunities. For example, local adaptation may change species' responses to resources and predation, affecting patterns of species interactions and coexistence (Kneitel 2002, Kneitel and Chase 2004) and ultimately affecting community dynamics in different *S. purpurea* populations (Ellison et al. 2003).

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